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Sympatry and syntopy of cichlids (Teleostei: Cichlidae) in the Selva Central, upper Ucayali river basin, Peru

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Abstract. Sympatry and syntopy are rare among congeneric cichlids in the Neotropics. Among Peruvian Amazonian cichlids congeneric syntopy has so far been reported in only 1 case known from a single locality. Based on thorough exploration of a new locality I refute the syntopy of the 2 species involved: *Bujurquina robusta* (Kullander, 1986) is a mouth-bay species while *B. labiosa* (Kullander, 1986) is an upland species. I demonstrate the generality of this ecological allotopy with further examples from a second study area including a different set of species.

Key words. Cordillera El Sira; Reservas comunal El Sira; Rio Tambo; Departamento de Ucayali; Rio Pachitea; Departamento de Pasco; congenerics.

Sympatry and especially syntopy are rarely reported among closely related congeneric cichlids in the Neotropics (Kullander 1983, Kullander 1986, Kullander & Nijssen 1989, Albert et al. 2011, pers. obs. based on field work in virtually all Neotropical countries). So far, cases of both congeneric sympatry and syntopy in Neotropical cichlids have only been documented in rare cases of adaptive radiations both in rivers (Piálek et al. 2012, Piálek et al. 2015, Říčan et al. 2016) and in lakes (Barluenga et al. 2006, Elmer et al. 2014), and only exceptionally in other cases, including the ones featured here. All of these reported cases of sympatry and syntopy contain species with disparate cranial morphologies suggesting divergence in alimentation modes. One of the rare cases of congeneric sympatry and syntopy that is not associated with any documented adaptive radiation is among Peruvian Amazonian cichlids in the genus *Bujurquina* (the *B. labiosa* and *B. robusta* species pair). *Bujurquina labiosa* (Kullander, 1986) is known from only one locality in the Ucayali river stretch close to Atalaya (Kullander 1986) while *B. robusta* (Kullander, 1986) is known from 3 separate localities (Kullander 1986, Carvalho et al. 2011). Congeneric sympatry without syntopy also appears to be rather rare in *Bujurquina* in the Peruvian Amazon with most species being allopatric (Kullander 1986). One additional case of sympatry in the upper Ucayali river basin apart from the *B. labiosa* and *B. robusta* species pair is in the Rio Pachitea basin including a different set of species of *Bujurquina* (Kullander 1986) and the sister genus *Tahuantinsuyoa* (Kullander 1986). Here, species are reported as allotopic except for one locality with possible syntopy (Kullander 1986). Among other cichlid genera in Peru sympatry is found in *Crenicichla* Heckel, 1840 where there are however species from 2 different species groups involved that, in ecological, morphological, and biogeographical sense, should best be treated as separate genera (Kullander et al. 2010, Piálek et al. 2012). In the studied area in Peru sympatry of species within the species groups of *Crenicichla* is absent, as is syntopy between the species groups (Kullander 1986, Říčan pers. obs.). Virtually all Peruvian cichlids are known chiefly from taxonomic contributions featuring their descriptions (Kullander 1986, Kullander 1991) and to my knowledge there are to this day no studies about the biology, habitat preferences, and, especially, large and small-scale biogeography of *Bujurquina* and *Tahuantinsuyoa*, the very common and dominant Peruvian cichlids.

Many presently known distributions reporting sympatry and syntopy are artifacts of sampling effort (e.g. Albert et al. 2011) and of not collecting systematically within a hypothesis-driven framework (for example, they do not seek out sufficient ecological and elevational gradients, such as is relevant to the present study). Using field observations from a new locality I demonstrate that the reported syntopy in the *B. labiosa* and *B. robusta* species pair is an observational and collection artifact since they occur syntopically in only a transition zone along the elevational gradient of the tributaries. Both species are, in fact, almost exclusively allotopic within the tributaries as observed along an elevational gradient within a stream in pristine condition in the vicinity of the Ashaninka village of Betania. This location also represents a new distributional record for both species along the Ucayali-Tambo river. *Bujurquina robusta* is a lowland lentic mouth-bay species while *B. labiosa* an upland lotic species. I further demonstrate the potential generality of this ecological allotopy in Peruvian Amazonian cichlids with further examples from a second study area around Puerto Bermúdez in the Rio Pichis–Pachitea river basin of the Ucayali drainage with a different set of species.

My comparisons between the two study sites show that ecologically mediated allotopy is likely a typical micro-

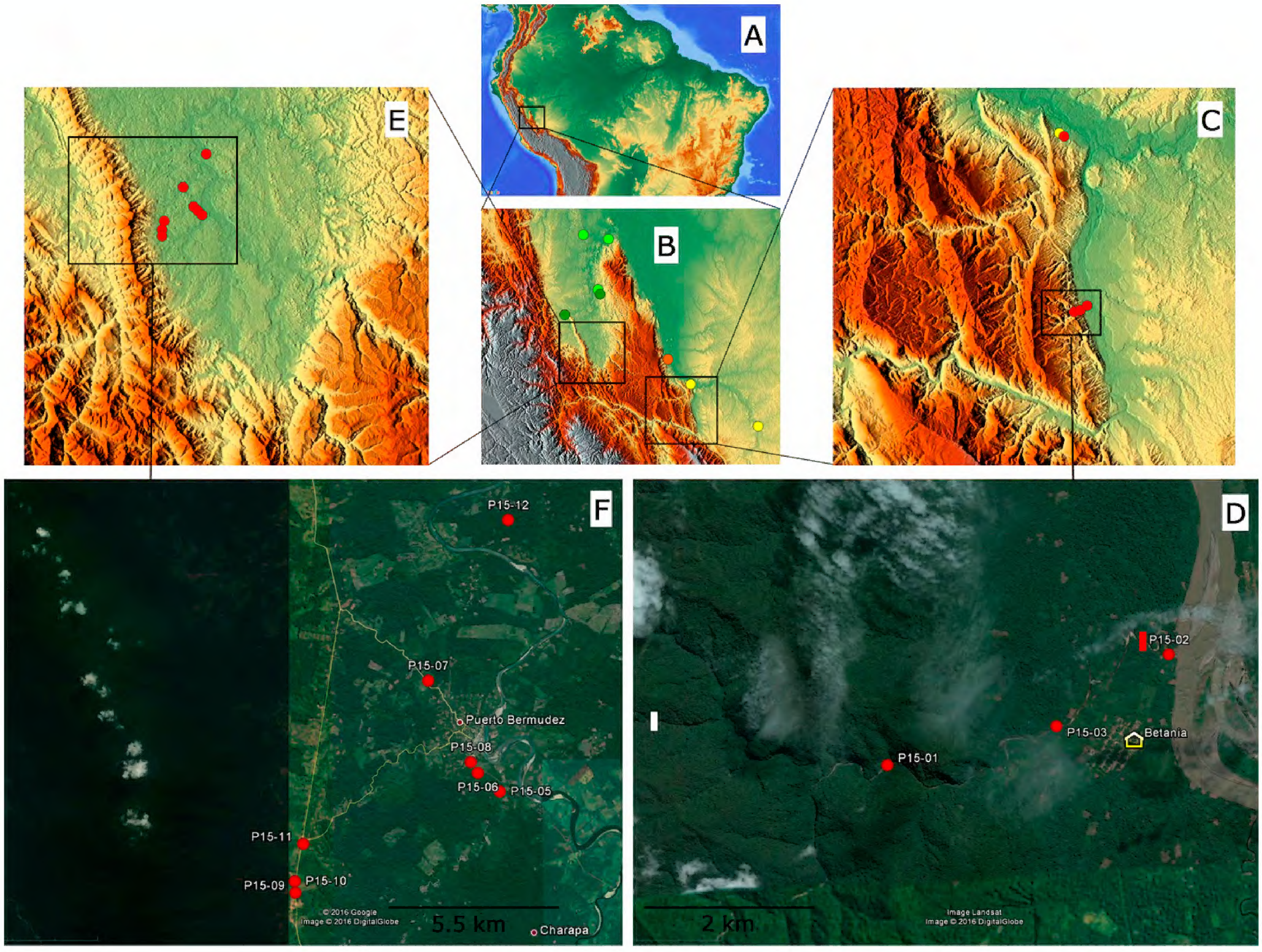

Figure 1. Maps of studied areas and collection records. **A.** Overview map showing location of the studied areas. **B.** Detail of the location showing the 2 collection areas around the Cordillera El Sira. Colored dots show previous collection records of the studied species. Dark green – *T. chipi*; light green – *B. megalospilus*; orange – *B. labiosa* and *B. robusta*; yellow – *B. robusta*. **C.** Topographic map and the studied locations in the Rio Ucayali-Rio Tambo. D. Satellite map of the studied area at Betania with collecting localities. Red bar marks boundary of lentic and lotic habitats; white bar marks the end of the explored part of the stream. **E.** Topographic map of studied locations in the Rio Pichis area around Puerto Bermúdez. **F.** Satellite map of studied area around Puerto Bermúdez with collecting sites.

distributional pattern of sympatric congeneric cichlids in the Selva Central of Peru.

Both study localities present new records of *B. labiosa*, *B. robusta*, *B. megalospilus* (Kullander, 1986), *Tahuantisuyoa chipi* (Kullander, 1991), *Aequidens patricki* (Kullander, 1984), and *Crenicichla sedentaria* (Kullander, 1986) (and the southernmost records for *B. megalospilus*, *T. chipi*, *A. patricki*) which are all narrow endemic species of the upper Ucayali and its main tributaries (Kullander 1986, Kullander 1991). This study also brings the first photographs of live specimens of *B. labiosa*, *B. robusta*, *B. megalospilus,* and *T. chipi,* supported by both voucher specimens and DNA tissue samples.

Two areas in the Selva Central were studied (Fig. 1; Table 1); one at the Ashaninka village of Betania (Quebrada Samaireni; 11°03′18.73″ S, 073°45′11.58″ W) at the left bank of the Rio Tambo (upper Rio Ucayali basin) and on the east slope of the Cordillera El Sira; the other around Puerto Bermúdez (10°17‘51.99″ S, 074°56′11.22″ W) on the opposite side of the Cordillera El Sira (Fig. 1) in the Rio Pichis-Pachitea basin (upper Rio Ucayali basin). I additionally collected in the Rio Tambo-Rio Ucayali basin at Quebrada Aerija (locality P15-04; see Table 1), a human-polluted stream close to the town of Atalaya (10°43′54.60″ S, 073°45′31.08″ W), and in the Rio Tambo canyon between Puerto Prado (11°09′9.75″ S, 074°14′25.91″ W) and Poyeni (11°15′18.21″ S, 073°40′6.04″ W).

At the 2 locations in the Rio Tambo-Rio Ucayali basin (Samaireni and Aerija) I observed the 2 *Bujurquina* species (*B. labiosa* and *B. robusta*) supposedly endemic to this stretch of the Ucayali river basin, plus another upper Ucayali endemic species, *C. sedentaria*, known to have a larger distribution (Kullander 1986). Other cichlids with wide distributions in Peru caught or observed at my localities are not treated in this study. The study site at Betania (Quebrada Samaireni) represents a new distribution record for all 3 species and widens their ranges into the Rio Tambo basin. The Quebrada Samaireni at Betania is in pristine condition (see Fig. 2) and I made observation of its cichlid fauna by walking the whole stream from its mouth into the Rio Tambo all the way to about 750 m above sea level (a.s.l.) (see Fig. 1). Throughout the stream I also made observations of the cichlid fauna by snorkling. Voucher

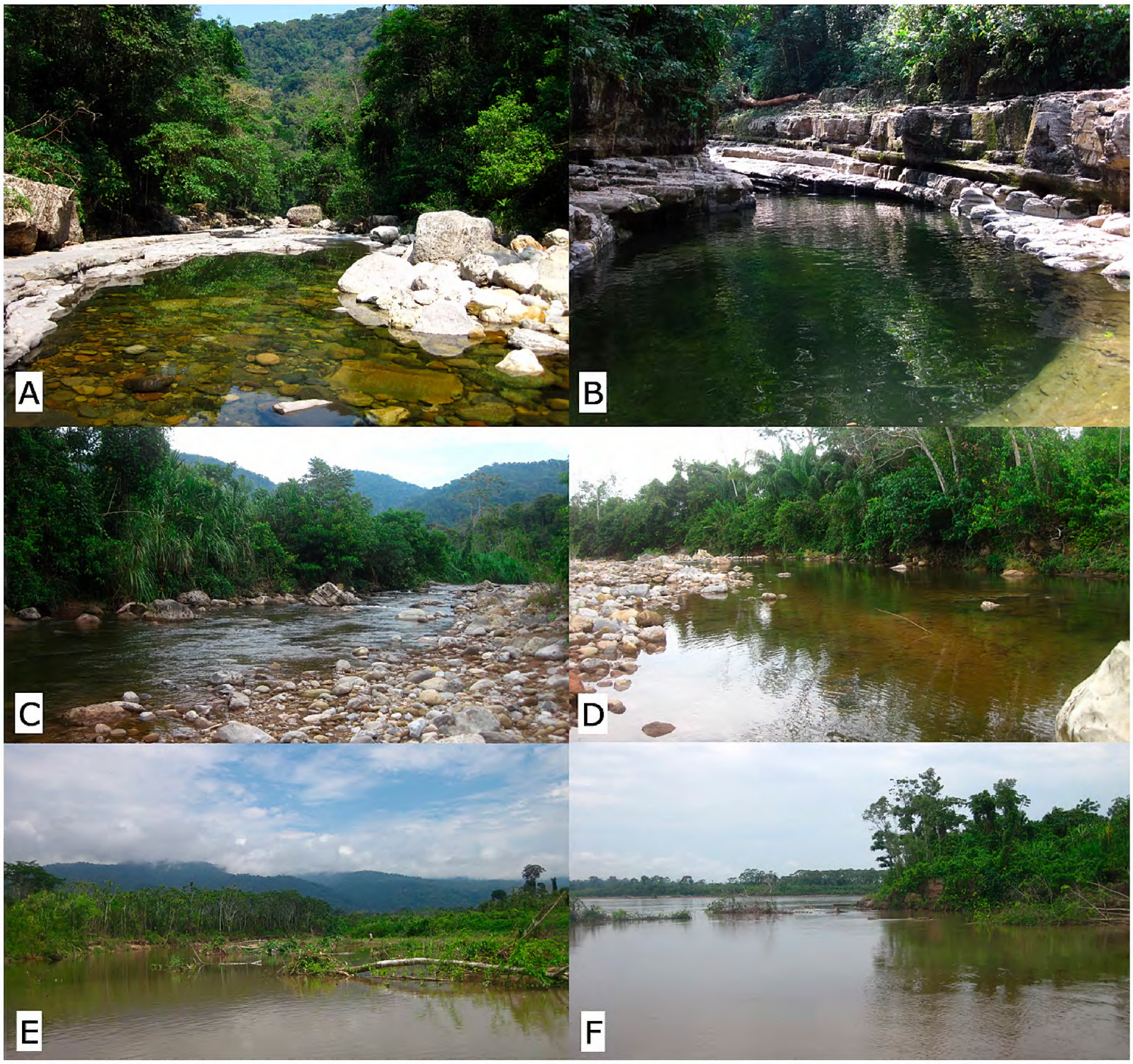

Figure 2. Studied localities and encountered *Bujurquina* species in Quebrada Samaireni at *Betania*. **A, B.** High elevation locality P15-01 (370 m a.s.l.; photos taken 26-9-2015) showing the semi-isolated pools within the steep river bed. The only *Bujurquina* species present was *B. labiosa*. **C, D.** Middle elevation locality P15-03 (260 m a.s.l.; photos taken 28-9-2015) showing the fast running clear-water stream and a pool. The only *Bujurquina* species present was *B. labiosa*. **E, F.** Low elevation locality P15-02 (242 m a.s.l.; photos taken 28-9-2015) close to the mouth into the Rio Tambo showing the slow flowing, turbid stream. The only *Bujurquina* species present was *B. robusta*.

specimens were collected at 3 localities along the stream (localities P15-01 to P15-03; Fig. 2 and Table 1). The uppermost locality within the stream (P15-01) marks the end of perennial water in the stream. Above this point, the river, during the dry season, holds water only in several pools isolated by hundreds of meters of dry stream bed. The pools are fed by water seeping from the rocks. Between the pools the water flows beneath the river bed. The uppermost locality is thus, based both on my observations and the character of the stream, the upper limit of cichlid distribution within the stream (confirmed by my Ashaninka guide). For the majority of its length the stream is fast flowing and crystalline with isolated pools and the stream bed composed of boulders, rubble, coarse gravel, and sand (Fig. 2). The stream has only a short lentic mouth-bay area with semiturbid to turbid water and a gravelly-sandy-muddy bottom. I studied the stream for 6 days between 25-9-2015 to 30-9-2015, just before the start of the rainy season during the lowest water levels (again confirmed by my Ashaninka guide).

During my boat journey to Betania and Atalaya I further explored the whole stretch of the Rio Tambo down from Puerto Prado. I found all tributaries of this stretch of the river down to Poyeni (where the river exits the Tambo canyon) dry during the dry season, which my Ashaninka guide confirmed as well. Cichlid distribution in these tributaries is thus ruled out; *B. labiosa*, due to its habitat requirements (see below), is likely not found upriver from Poyeni. *Bujurquina robusta* is more

likely to occur above Poyeni in the main channel, where I was however not able to collect or observe any specimens. The general rule based on my field work is that these and most other cichlids are rare in the main rivers compared to the tributaries.

The second study site was around Puerto Bermúdez in the Rio Pichis-Pachitea tributaries (also upper Rio Ucayali basin) where I studied localities along the elevational gradient to the spur running from the Bosque de Protección San Matías-San Carlos located on the opposite side of the Cordillera El Sira (Fig. 1). See Table 1 for geographic (GPS) coordinates, eleva-

Table 1. Locality and specimen information.

River basin	Locality description	Elev. (m)	Geographic coordinates	Locality	All observed cichlid spp. (rare species)	Species	Voucher MUSM tag
Rio Tambo	Upland pools in Quebrada Betania (upland habitat)	370	11°03'24.91"S, 73°46'49.05"W	P15-01	*Bujurquina labiosa*, (*Crenicichla sedentaria*)	*Bujurquina labiosa*	P15-01-01-686
						Bujurquina labiosa	P15-01-02-juvet
						Bujurquina labiosa	P15-01-03-juvet
						Bujurquina labiosa	P15-01-04-688
						Bujurquina labiosa	P15-01-05-689
						Bujurquina labiosa	P15-01-06-691
Rio Tambo	Quebrada Betania at mid-elevation on road Betania - Atalaya (upland habitat)	260	11° 3'8.70"S, 73°45'36.40"W	P15-03	*Bujurquina labiosa*, (*Crenicichla sedentaria*)	*Bujurquina labiosa*	P15-03-18-704
						Bujurquina labiosa	P15-03-19-706
						Bujurquina labiosa	P15-03-20-707
						Bujurquina labiosa	P15-03-21-708
Rio Tambo	Mouth of Qubrada Betania into Rio Tambo (lowland habitat)	242	11° 2'38.18"S, 73°44'47.62"W	P15-02	*Bujurquina robusta*, (*Crenicichla sedentaria*)	*Bujurquina robusta*	P15-02-08-695
						Bujurquina robusta	P15-02-09-694
						Bujurquina robusta	P15-02-10-696
						Bujurquina robusta	P15-02-11-697
						Bujurquina robusta	P15-02-12-698
						Bujurquina robusta	P15-02-13-699
						Bujurquina robusta	P15-02-14-700
						Bujurquina robusta	P15-02-15-701
						Crenicichla sedentaria	P15-02-07-693
Rio Ucayali	Quebrada Aerija by Atalaya (antropogenically polluted upland habitat)	235	10°42'41.28"S, 73°47'44.60"W	P15-04	*Bujurquina robusta*, (*Bujurquina labiosa*)	*Bujurquina robusta*	P15-04-23-710
						Bujurquina robusta	P15-04-24-711
						Bujurquina robusta	P15-04-25-712
						Bujurquina robusta	P15-04-26-713
						Bujurquina robusta	P15-04-28-715
						Bujurquina labiosa	P15-04-27-714
						Bujurquina labiosa	P15-04-29-716
Rio Pichis	Upland part of main left tributary above Puerto Bermudez (upland habitat)	262	10°20'23.60"S, 74°59'16.10"W	P15-09	*Tahuantinsuyoa chipi*	*Tahuantinsuyoa chipi*	P15-09-41-727
Rio Pichis	Upland small blackwater pool between locs 09 and 11 (rainforest habitat)	265	10°20'12.20"S, 74°59'16.70"W	P15-10	*Aequidens patricki*	*Aequidens patricki*	P15-10-42-728
Rio Pichis	Upland part of main left tributary above Puerto Bermudez (upland habitat)	260	10°19'34.90"S, 74°59'8.00"W	P15-11	*Tahuantinsuyoa chipi*	*Tahuantinsuyoa chipi*	P15-11-43-729
						Tahuantinsuyoa chipi	P15-11-44-730
Rio Pichis	Blackwater pool on a small stream between locs 05 and 08 (rainforest habitat)	247	10°18'24.70"S, 74°56'10.40"W	P15-06	*Aequidens patricki*	*Aequidens patricki*	P15-06-31-718
						Aequidens patricki	P15-06-32-720
						Aequidens patricki	P15-06-39-juv
						Aequidens patricki	P15-06-40-juv
Rio Pichis	Quebrada Chincoreani within lowland forest (rainforest habitat)	260	10°14'12.10"S, 74°55'38.70"W	P15-12	*Aequidens patricki* (*Tahuantinsuyoa chipi*, *Crenicichla sedentaria*)	*Aequidens patricki*	P15-12-45-731
						Aequidens patricki	P15-12-49-735
						Aequidens patricki	P15-12-50-736
						Aequidens patricki	P15-12-51-737
						Aequidens patricki	P15-12-47-733
						Tahuantinsuyoa chipi	P15-12-46-732
						Crenicichla sedentaria	P15-12-48-734
Rio Pichis	Main left tributary of Rio Pichis above Puerto Bermudez close to mouth into Rio Pichis (lowland habitat)	243	10°18'43.40"S, 74°55'48.20"W	P15-05	*Bujurquina megalospilus*	*Bujurquina megalospilus*	P15-05-30-717
						Bujurquina megalospilus	P15-05-52-738
						Bujurquina megalospilus	P15-05-53-739
						Bujurquina megalospilus	P15-05-54-740
						Bujurquina megalospilus	P15-05-55-741
Rio Pichis	Small left tributary of Rio Pichis above Puerto Bermudez (lowland habitat)	244	10°18'13.85"S, 74°56'17.40"W	P15-08	*Bujurquina megalospilus*, (*Tahuantisuyoa chipi*, *Crenicichla sedentaria*)	*Bujurquina megalospilus*	P15-08-37-725
						Bujurquina megalospilus	P15-08-56-742
						Bujurquina megalospilus	P15-08-57-743
						Bujurquina megalospilus	P15-08-58-744
						Bujurquina megalospilus	P15-08-60-746
						Bujurquina megalospilus	P15-08-61-747
						Tahuantinsuyoa chipi	P15-08-59-745
						Crenicichla sedentaria	P15-08-38-726

Figure 3. Studied localities in the tributaries of the Rio Pichis at Puerto Bermúdez. A, B.High elevation locality P15-09 (262 m a.s.l.; photos taken 4-10-2015) showing the fast running, clear-water stream and a pool. The only cichlid species present was *T. chipi*. C, D. Rainforest stream locality P15-12 (260 m a.s.l.; photos taken 5-10-2015) showing habitat heterogeneity. Four cichlid species were found at this locality (the common rainforest species *A. patricki*, and the rare *T. chipi*, *B. megalospilus*, and *C. sedentaria*). E, F. Low elevation locality P15-05 (243 m a.s.l.; photos taken 6-10-2015) close to the mouth into the Rio Pichis showing the slow flowing, semi-turbid stream. The only *Bujurquina* species present was *B. megalospilus*.

tion and other data on the localities. Within the Rio Pachitea basin of the Ucayali drainage several narrow endemic species of *Bujurquina* and the closely related *Tahuantinsuyoa* have been reported together with *C. sedentaria* and additionally with *A. patricki*. Most of the species are reported as allotopic within the the Pachitea basin (Kullander 1986). Detailed habitat preferences for the species have again not been reported, but at at least 1 site several species have been reported in possible syntopy (Kullander 1986). In the study area around Puerto Bermúdez I studied several tributaries and localities (P15-05 to P15-12) during 5 days from 2-10-2015 to 6-10-2015 at the end of the dry season during lowest water levels. The streams and localities were again explored by both fishing and observation (including snorkling where possible). The elevational gradient was studied by comparing the different localities and also along the largest tributary with the largest gradient (between the lowland locality P15-5 and the upland localities P15-9 to P15-11; Figs. 1, 3; Table 1). The elevational gradient was again studied by walking the length of the largest stream, in this case not in its entirety but only from the mouth into the transitional stage between the lowland and upland habitats, and then in the upland localities (P15-9 to P15-11). The lowland-upland boundary is in this stream much less pronounced compared to the Rio Tambo-Rio Ucayali left-hand tributaries (Fig. 1). The upland localities P15-9 and P15-11 are again characterized by strongly flowing clear water with a bouldery bottom and rare pools

(Fig. 3) and are also at the uppermost limit of cichlid distribution within this tributary since the streams above these points carry very little water and are extremely shallow during the dry season. Localities P15-07, P15-10, and P15-12 are on shaded slow-flowing rainforest streams with sandy-muddy bottom and lots of submerged wood (I had no success in collecting cichlids at P15-07 despite the river looking healthy and suitable for them), while P15-05 and P15-08 are lowland stretches with exposed sky, close to mouths into the Rio Pichis, with gravelly-sandy-muddy bottoms and semiturbid to turbid water. Locality P15-06 is a human-made pool in a deforested cattle patch on a very small (originally rainforest) stream. I observed and collected in the study area around Puerto Bermúdez 1 *Bujurquina* species (*B. megalospilus*) and 1 *Tahuantinsuyoa* species (*T. chipi*) together with *C. sedentaria* and *A. patricki*. My *B. megalospilus*, *T. chipi,* and *C. sedentaria* records from around Puerto Bermúdez represent the first records of these species in the Rio Pichis drainage. Previously they were reported this far upstream only from the Rio Palcazú (Kullander 1986), which together with the Rio Pichis forms the Rio Pachitea.

Fishes were collected under a permanent permit to Hernán Ortega, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru. Specimens were obtained by fishing using cast nets and gill nets in all available microhabitats at all localities. Localities were chosen specifically so that they capture the full regional ecological habitat variation of the two main studied areas and so that they especially capture elevational gradients within single tributaries at both studied areas. At localities with sufficient visibility (all upland and rainforest streams and some lowland locations) direct observation of the fish fauna was carried out using mask and snorkel.

Collected specimens (Table 1) were individually and permanently tagged and a DNA tissue sample taken from their right pelvic fin. DNA tissue samples were preserved in 1.5 ml Eppendorf Safe lock tubes in absolute ethanol and deposited at the fish tissue collection of the Department of Zoology, Faculty of Science, University of South Bohemia in České Budějovice, Czech Republic. Specimens were preserved in 10% formalin and later transferred to 70% ethanol and deposited at the fish collection of the MUSM, Lima, Peru.

Species were determined using the original taxonomic descriptions (Kullander 1986, Kullander 1991) that include the only review work (Kullander 1986) on the cichlid fauna of Peru. Morphological data are also compared with Kullander (1986). Detailed comparative ecomorphological analyses and molecular phylogenetic analyses are deferred to special publications.

Bujurquina labiosa and *B. robusta* were originally known from only 2 and 8 specimens, respectively, collected at a single locality (with the exception of 1 *B. robusta* specimen), a backwater on the R. Chinipo near Chicosa in the upper R. Ucayali (Kullander 1986). *Bujurquina labiosa* is actually solely known from this locality while specimens referred to as *B. robusta* have been reported from a wider area reaching into the Urubamba tributary of the upper Ucayali (Carvalho et al. 2011) and is so far known from 3 separate areas (localities; Fig. 1).

Bujurquina labiosa is readily distinguished from all other *Bujuquina* species by the possesion of conspicuously long, pointed head and snout and hyperdeveloped lips. It is further distinguished from the only sympatric species *B. robusta* by the following combination of characters confirmed in my specimens: head length (37% of standard length (SL) vs. 32–35.0%), slenderer body (depth 39% vs. 41–45% of SL), narrower interorbital (9–10% vs. 10.5–13% of SL), slenderer (and longer) caudal peduncle (depth 16% vs. 16.5–18% of SL), and shorter pectoral fin (length 28.5% of SL, vs. 30–34%).

Live coloration of *B. labiosa* was previously unknown. The live coloration of my specimens (Fig. 4) differs from the description of preserved specimens by Kullander (1986) chiefly in having prominent horizontal opalescent blue lines, with 2 lines of these per 1 longitudinal series of scales (1 opalescent line through the dorsal part of the scale and 1 through the ventral part of the scale with the central part of the scale darkly pigmented). This is the same pattern as in *B. robusta*, where it is, however, more distinctly and symmetrically developed. In both species the opalescent lines are chiefly limited to below the upper lateral line. The blue coloration in *B. labiosa* is always darker than in *B. robusta*, in which it grades either into silvery or light golden. The opalescent blue head markings are also darker than in *B. robusta*, as are the leading edges of the ventral fins. In coloration *B. labiosa* is most different from *B. robusta* in almost completely lacking any traces of the suborbital stripe, which at best is visible only as a very diffuse blotch just below the eye. This condition corresponds to the only well preserved specimen of Kullander (1986). Another coloration character that well separates *B. labiosa* from *B. robusta* are the vertical bars, which in *B. labiosa* are much narrower and more distinct than in B. *robusta* (Fig. 4), again corresponding to the specimen shown in Kullander (1986).

The diagnosis of *B. robusta* given by Kullander (1986) also corresponds well to my specimens: 24 scales in a horizontal series above that including the lower lateral line (E1 scales); jaws equal anteriorly; lips thin; pectoral fin short, 30–33% of SL; lateral band usually continuous, running toward dorsal-fin; bars 5 and 6 separate; vertical suborbital stripe faint but not completely faded with increasing size; no preopercular spot; nape band strong; bar 7 blotch-like; posterior dorsal-fin lappets black with white edge; and otherwise spinous dorsal fin immaculate.

Live coloration of *B. robusta* was previously unknown from specimens confidently identified as *B. robusta*. A *Bujurquina* species photographed underwater by Vierke (1983a, b) was referred to as *B. robusta* by Kullander (1986). The description of the live coloration by Kullander (1986) mostly corresponds to my specimens. *Bujurquina robusta* live coloration (Fig. 4) differs from the preserved coloration chiefly in having prominent horizontal opalescent blue lines with 2 lines of these per 1 longitudinal series of scales (as in *B. labiosa*; see above). The prominent buccal lines (1 and 2) and dots are also bright, light blue, as in most other *Bujurquina*. The anterior edge of the pelvic fin is contrastingly white, again as in most *Bujurquina*. Contrary to Kullander (1986), observing from the color photographs of Vierke (1983a, b), both the spinous dorsal fin as well as the soft dorsal fin in my specimens are edged orange (Fig. 4) versus "spinous dorsal fin appears white-

Upland species in clear lotic stretches

Species occuring in **rainforest streams at middle elevations** representing increased diversity and faunal mix

Lowland species in semi-turbid lentic stretches close to mouths into major rivers

Figure 4. Sympatry and syntopy of cichlids in the Selva Central of Peru. Upper row. Upland species solely occuring in clear lotic stretches of tributaries. Middle row. Species occuring in rainforest streams at middle elevations representing increased diversity and faunal mix. Lower row. Lowland species solely occuring in semi-turbid lentic stretches of tributaries close to mouths into major rivers. MUSM voucher tag numbers of the photographed specimens: *A. patricki*, P15-10-42-728; *B. labiosa*, P15-03-19-706; *B. megalospilus*, P15-05-52-738; *B. robusta*, P15-02-12-698; *T. chipi*, P15-09-41-727.

edged, the soft dorsal fin red-edged." All fins are light orange and the cheek has more orange tones than the body. The diagnostically very important suborbital stripe (Kullander 1986) in *B. robusta* is highly diffuse, not well developed, and long. In adults it is almost absent but more visible in juveniles. This is in strong contrast with the blotch-like remains of the suborbital stripe in *B. labiosa* (see above).

Bujurquina megalospilus, *Tahuantinsuyoa*, and *A. patricki* have previously been reported only from several localities within the Rio Pachitea basin and the adjacent Rio Aguaytia, both tributaries of the upper Ucayali. *Tahuantinsuyoa* has been split into two species, each supposedly endemic to each of the two tributary basins (Pachitea and Aguaytia; Kullander 1991), while *B. megalospilus* and *A. patricki* are treated as single species in both these non-communicating tributaries (Kullander 1986).

Bujurquina megalospilus has been diagnosed (Kullander 1986) by 23 E1 scales; jaws equal anteriorly; lips thin; pectoral fin long, 37.2–40.6% of SL; lateral band usually discontinuous; lateral blotch dominant flank marking; bars 5 and 6 separate; suborbital stripe vertical, indistinct in adult; no preopercular spot; nape band indistinct; bar 7 blotch-like; posterior dorsal-fin membranes dark with hyaline base, spinous dorsal fin otherwise immaculate. This diagnosis is well reflected by my specimens except that in none of my (live) specimens the lateral blotch (that gave the species its name) is well developed and so cannot be named as a dominant flank marking (see below that comparisons of live coloration versus preserved coloration do clarify this conflict). Since my specimens also represent a new distribution record, I intend to collect at the type locality and other close localities in coming years to further ascertain the species status of the specimens reported here.

Kullander (1986) described the live coloration of his specimens but did not provide color photographs and thus comparisons can only be made with the description of the coloration. The holotype, when freshly collected, was white on chest, abdominal sides, and lower sides of head. My specimens are also whitish in these areas but this is uninformative since most *Bujurquina* (indeed, cichlids and fish in general) are whitish ventrally. My specimens (Fig. 4) have a distinctive orangish to bright orange background coloration with golden margins (or dots) of the midlateral blotch and the dark stripe anterior from the blotch. Kullander does not report any of this interesting and diagnostic coloration but reports that "near lateral spot, which

not well discernible in live specimens, three scales with large silvery spots." This pattern refers to what I consider a diagnostic feature of my specimens and hence of *B. megalospilus*. The species name *megalospilus* is thus rather inappropriate since the large midlateral blotch is only a feature of preserved specimens when all other markings have faded. Most of my preserved specimens indeed have a prominent midlateral blotch. Kullander's specimens have head, back, and sides overall light café-au-lait (Kullander 1986). This coloration is not that different from my specimens (which are orange) and could be attributed to a slightly different part of the dry season of Kullander's specimens, water conditions (e.g., turbidity), and/or especially geographical distance, since my specimens are those most geographically removed. Buccal stripes 1–2 are bluish in my and in Kullander's specimens, as is the black iris, with light, reddish spot dorsally (in my specimens anterodorsally), and pupil ring golden (as in most *Bujurquina*). Suborbital stripe barely indicated in my specimens and similar to the other two featured *Bujurquina* species, but more similar to *B. labiosa* in being limited to just below the eye. Lateral band is dull black and vertical bars are faintly grey, showing on back only in my specimens. The usual opalescent horizontal lines of most *Bujurquina* are also light blue in my specimens, but arranged differently than in *B. labiosa* and *B. robusta* described above. In my specimens they run throught the center of the scales, and thus there is only 1 opalescent line per 1 horizontal scale series. This corresponds to what Kullander reported as "middle lateral line scales with silvery dot near tube." Also unlike the previous two *Bujurquina* the opalescent lines are only present ventrally from the mid-lateral blotch (versus ventrally from the upper lateral line). The overall expression of the opalescent markings is much less than in *B. labiosa* and in *B. robusta* (where they dominate the live coloration) both on the body and head. Fins are light oranage, as in both of the previous *Bujurquina* (and as in Kullander's specimens). The ventral fin also has a white leading edge.

Tahuantinsuyoa is, based on present knowledge (Musilová et al. 2008, Musilová et al. 2009), the sister genus of *Bujurquina*. *Tahuantinsuyoa chipi* is very similar to its sister species *T. macantzatza* (Kullander, 1986), differing in having a dark spot on the head (adjacent to the posterosuperior orbital rim), instead of a caudal-inclined dark nape band (connected with the transversal band posteriorly), and in having a long dark suborbital stripe below the eye of about uniform width, instead of one which is distinctly wider ventrally. This diagnosis of *T. chipi* well corresponds to my specimens (Fig. 4) even though the separate species status of the population might be seen questionable since the differences are very slight. My work, including phylogenomic analyses, will soon shed more light on this question. The long and well-pigmented suborbital stripe is the chief coloration pattern distinguishing *Tahuantinsuyoa* from *Bujurquina* in the area studied here (Fig. 4).

Live coloration of *T. chipi* has not been reported in ichthyological literature so far, but the species is very similar to its sister species based on my specimens and on the original description. The coloration pattern of the 2 species, besides 2 distinguishing features, is virtually identical. These distinguishing features become best evident in breeding coloration in which *Tahuantinsuyoa* become almost completely white (unlike any *Bujurquina* species where breeding coloration is known) with the suborbital stripe and nape band contrasting black. The posterior inclination of the nape band in *T. Macantzatza* also becomes much more visible (versus anterior inclination in *T. chipi*) (see also http://www.cichlidae.com).

Aequidens patricki is hard to confuse with any other Peruvian cichlid and easily identified using the original description (Kullander 1984) which also features pictures of live specimens. My specimens (Fig. 4) reflect well the diagnosis and the photographs of those live specimens.

Crenicichla sedentaria is also a distinctive species among Peruvian *Crenicichla* that is hard to confuse (Kullander 1986); it is readily separated by large flank scales (less than 70 in *C. sedentaria* versus 100 in *C. johanna*, Heckel 1840, and *C. cincta*, Regan 1905) and dental shape and colour features (inner teeth depressible, head compressed, absence of humeral blotch and suborbital stripe present in *C. saxatilis* (L. 1758) species group). My specimens (Fig. 5) fit well to the diagnosis and the photographs of the live specimens, which, though not reported by Kullander in the original description, are available in several publications including online sources (e.g., http://www.cichlidae.com) and are hard to confuse since this is such a distinctive species. Kullander (1986) gave the name *sedentaria* because tentativelly identified aquarium specimens (without locality information and general area of origin, but most likely from Colombia) were seen resting on the bottom. The species name *sedentaria* based on my results is rather misleading since I exclusively observed normal swimming behaviour in the species in the wild as in most other *Crenicichla* (unlike the benthic specialists from the Tocantins and Xingu rivers) and since the species is found to be ecotopically generalistic in all habitats studied.

Bujurquina labiosa has been reported as syntopic with *B. robusta* (at the previously only known locality in the Rio Chinipo, from Staeck & Linke 1985), from which it differs strikingly in mouth structures. This led Kullander (1986) to suggest that the co-existence is associated with different trophic habits. Kullander himself did not visit the site and all information was taken from Staeck & Linke (1985) who provided the specimens as well as locality and habitat observations. My data support the distinctiveness of the 2 species (see above and Fig. 4) but I did not find or observe them in syntopy in my elevational study along the pristine Quebrada Samaireni by Betania in the Rio Tambo drainage (Figs. 1, 2; localities P15-01–03; Table 1). I have only found them in syntopy in the human-polluted Quebrada Aerija close to the town of Atalaya (locality P15-04; see Table 1). Within the Quebrada Samaireni at Betania, *B. robusta* is limited to the lowermost portion of the stream with reduced to no flow close to the mouth of the Rio Tambo. This stretch of the stream is characterized by turbid slow flowing water with a gravelly-sandy-muddy bottom (Fig. 2). On the other hand I observed *B. labiosa* throughout the rest of the stream up to locality P15-01 (vouchers and DNA samples were also collected at P15-03; Figs. 1, 2). This whole stretch of the stream is characterized by long sections of fast flowing clear water with bouldery bottoms interspersed with rather rare pools, in which the concentration of *B. labiosa* was the highest

Figure 5. Adult and juvenile *Crenicichla sedentaria.*

(Fig. 2). *Crenicichla sedentaria* was observed throughout the stream from its mouth to the uppermost locality and does not seem to have as strict habitat requirements as either of the 2 *Bujurquina* species.

The Quebrada Samaireni near Betania is typical for the whole stretch of left-hand tributaries of the Rio Tambo-Upper Rio Ucayali. All these left-hand tributaries (including Quebrada Samaireni, the Rio Chinipo and Quebrada Aerija) show the same marked elevational gradient (Fig. 2) with markedly different habitat characteristics of the lowermost and the remaining stretches. The streams have short lowland stretches close to the mouth into the Rio Tambo–upper Rio Ucayali while most of their lengths have upland (highland) characteristics. Both *B. labiosa* and *B. robusta* appear to be endemic to this portion of the upper Ucayali river basin (including the lower Urubamba in *B. robusta*), with *B. labiosa* being an upland species while *B. robusta* is a lowland species. Following my observations the reported syntopy of the 2 species does not exist or at least is very rare in pristine streams with sharp lowland-upland transition zones (such as Quebrada Samaireni near Betania). However, in human-modified streams (such as Quebrada Aerija), or in longer streams with more protracted lowland–upland transitions, the 2 species can be found in syntopy in the transition zone. The previously known locality of both species on the Rio Chinipo is said to be on a farm and the stream was not surveyed in the same systematic manner as in my study of Quebrada Samaireni near Betania. The syntopy of the 2 *Bujurquina* species thus appears rare and the different trophic habits (as postulated from the different morphology) are not the result of co-existence but of different ecological habitats that each of the species inhabits. These habitats occur in allotopy along the elevational gradients of the tributaries of the Rio Tambo–upper Rio Ucayali.

Bujurquina megalospilus, *B. hophrys* (Kullander, 1986), *B. apoparuana* (Kullander, 1986), *T. chipi*, *A. patricki*, *A. tetramerus* (Heckel, 1840) and *C. sedentaria* have previously been reported as sympatric in the Rio Pachitea river basin (Kullander 1986). However, at most localities only 1 of the species was collected suggesting allotopy (or collection bias). At 1 location, Panguana in the Rio Llullapichis, a tributary of the middle Pachitea, Kullander (1986, 1991) reported 3 species (*B. megalospilus*, *B. hophrys* and *T. chipi*). The species were collected by Lüling (1981) and not by Kullander himself, who did not visit this site or the area, and, most important here, Lüling (1981) provides information that the specimens were collected in a wider area than just at the research station at Panguana. The syntopy of the species at Panguana is thus only conjectural.

At my study site in the Rio Pichis tributary basin around Puerto Bermúdez I only found a subset of these species (*B. megalospilus*, *T. chipi*, *A. patricki*, and *C. sedentaria*). The missing species (*B. hophrys*, *B. apoparuana*, *A. tetramerus*) thus very likely do not reach this high up into the Rio Pachitea basin. I collected most of the species in allotopy (in agreement with the results of previous studies). Based on my study syntopy of the species is thus indeed rare and not a collection bias. The only habitat in which all the 4 species could be found in syntopy were small, shaded rainforest streams with moderate current velocities and lots of habitat heterogenity in the form of rubble, sand, and mud on the bottom, fallen logs, wood, and both small riffles and pools. By far the dominant species here is *A. patricki;* I have not been able to collect or observe this species in my study area in any other stream type.

On the other hand, I only found *B. megalospilus* in lowland open-sky semi-muddy mouth areas of tributaries. It will probably be also present in pools in the main river (though my collections there were not successful).

Tahuantinsuyoa chipi is found virtually only in upland stretches of the tributaries in pools and in the strongly flowing clear water over bouldery bottoms. I collected a few specimens in the rainforest streams, but not in the lowland mouth areas. *Tahuantinsuyoa chipi* and *B. megalospilus* are thus completely allotopic to the same extent and with the same habitat preferences and morphologies as *B. labiosa* and *B. robusta* (Fig. 4).

As in the Rio Tambo area I observed and collected *C. sedentaria* throughout the various habitats and localities without clear habitat preferences.

My comparison between the 2 study sites (Betania and Puerto Bermúdez) shows that allotopy is a typical micro-distributional pattern of cichlids within individual streams in the Selva Central of Peru. In my study area, upland and lowland species are separated at elevational and ecological transition zones within single tributaries which are well reflected in the ecomorphology of the lowland (lentic) and upland (lotic) species, each of which are represented by a distinct morphology (Figs. 2–4). Upland species living in fast-flowing, clear-water streams with bouldery bottoms have thick lips, long heads, large mouths, longer jaws, preorbital distance, streamlined body, long caudal peduncle, and short streamers on pelvic fins (lotic ecomorphology), while lowland species living in proximity to mouths into large (here, always turbid) rivers in slow flowing to stagnant semi-transparent to muddy streams with gravelly-sandy-muddy bottoms have thin lips, short heads, smaller mouths, shorter jaws, preorbital distance, deep body, short caudal peduncle, and long streamers on pelvic fins (lentic ecomorphology; Fig. 4). The long head and thick lips in *Tahuantinsuyoa* are associated with stout pharyngeal teeth and the species are thought to be at least partially molluscivorous. The condition of the pharyngeal teeth in *B. labiosa* is unknown and presently under investigation to determine whether the supposed parallelism is also functional (but see notes below on phylogenetic relationships).

Small short streams with steep gradients (such as Quebrada Samaireni by Betania) have very sharp and short transition zones between lentic and lotic habitats (and hence cichlid ecomorphs) while in longer tributaries the transition zone is less pronounced and more diffuse, enabling overlap between the lentic and lotic ecomorphs.

Rainforest streams at intermediate elevations (in between the upland portions and the mouths) and ecologies (moderate flow, mixture of lowland and highland bottom types, etc.) have rich faunas that have additional cichlids (e.g., *Aequidens* species in the studied case) as well as both the upland and lowland species at low densities (Figs. 3, 4).

This complexity of habitats (even within individual streams) and species restricted to them enables the existence of the large sympatric diversity of Amazonian cichlids. This biogeographical complexity needs to be taken into account when conducting and interpreting phylogenetic, phylogeographic, and biogeographic studies on cichlids in the Amazon.

From a systematic and taxonomic point of view the ecomorphological dichotomy between lotic and lentic ecomorphs in the fishes studied is reflected at 2 levels: between the lotic genus *Tahuantinsuyoa* and the predominantly (and likely ancestrally) lentic genus *Bujurquina*, and within the genus *Bujurquina*, most strongly between *B. labiosa* and its sister group or sister species, which are currently unknown but pending a molecular phylogenetic analysis currently being conducted (Říčan et al. in prep.). *Bujurquina labiosa* has not been studied for those anatomical characters that supposedly separate *Bujurquina* and *Tahuantinsuyoa* (Kullander 1986, Kullander 1991), nor was it included in the previously conducted molecular phylogenetic studies that found the 2 genera as sister groups (Musilová et al. 2008, Musilová et al. 2009). Apart from very few anatomical characters, virtually all external characters separating *Tahuantinsuyoa* from *Bujurquina* are ecomorphological characters not reflecting phylogeny but only habitat preferences (Říčan et al. 2016, this study). All of these are identical between *Tahuantinsuyoa* and *B. labiosa* (Kullander 1996), as already demonstrated by morphological phylogenies (Musilová et al. 2009). Morphological phylogeny with ordered multistate characters, which emphasizes ecomorphological characters (since most are meristic or body shape characters, hence, multistate), place *B. labiosa* as the sister species of *Tahuantinsuyoa,* which is an inner group of *Bujurquina* (Musilová et al. 2009). Only analyses with unordered multistate characters find the 2 genera monophyletic with the similarity between *Tahuantinsuyoa* and *B. labiosa* interpreted as convergence (Musilová et al. 2009). The few critical anatomical characters separating *Tahuantinsuyoa* and *B. labiosa* have not been checked in *B. labiosa* and thus it remains to be demonstrated that they are not ecomorphological characters as well and whether there is merit in keeping *Tahuantinsuyoa* as a separate genus from *Bujurquina*. The breeding coloration of *B. labiosa* is presently unknown but is very important to investigate and compare it with the supposedly diagnostic white breeding coloration of *Tahuantinsuyoa*. In Middle American cichlids it has been found that the breeding colorations with the greatest amount of pure white coloration are also found in species from highland clear-water streams while lowland species from more turbid waters have more obscured breeding colorations (Říčan et al. 2016).

The lentic–lotic ecomorphological dichotomy within *Bujurquina* (and between *Bujurquina* and *Tahuantinsuyoa*) in a clear sympatric setting is so far only known from the studied

area in the upper Ucayali river basin (Kullander 1986, this study). Whether the absence of this phenomenon elsewhere within the large distribution of *Bujurquina* is real or just a sampling artifact remains to be investigated within this hypothesis-driven framework. If it should turn out as real, its presence within the upper Ucayali then remains to be explained.

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